ASTACOCROTON, A NEW TYPE OF ACARID.

By W. A. HASWELL, M.A., D.Sc., F.R.S., Emeritus Professor of Biology,
University of Sydney.

(Plates xxxvi.-xxxvii.)

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1. Introductory; mode of occurrence, methods, etc.

The Acarid dealt with in this paper occurs, sometimes abundantly, in the branchial chambers of the common spiny Crayfish (*Astacopsis serratus*) of the rivers of Eastern Australia. I have found it most numerous in the bright crimson variety that frequents the larger tributaries of the Grose and Cox in the Blue Mountains; but it occurs also, though more rarely, in the Crayfishes of small streams not connected with the Hawkesbury River system.*

The adult females, which are devoid of eyes, are firmly attached to the gill-filaments of their hosts by means of the chelicerae and pedipalpi, and can only be detached by the use of a certain amount of force. The males, which are comparatively small, and which are provided with a pair of eyes, are not attached, but swim very actively. Probably they are intermittently parasitic, though I have no actual direct evidence of this. The same holds good of the young females. Though soft and thin-skinned, *Astacocroton* is by no means easily acted on by fixing agents. In cold sublimate-acetic or alcohol it remains

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**Astacocroton does not occur on the common bicarinate Crayfish or "Mirami" *(Parachaeraps bicarinatus)*; and a number of specimens of the Western Australian *Chaeraps tenuimanus*, *C. quinquecarinatus* and *C. preissii* examined by me with the assistance of Mr. F. A. McNeill, Zoologist in charge of Lower Invertebrates at the Australian Museum, proved also to be free from the parasite.

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[Read 30th August, 1922.]

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alive for a long time and eventually undergoes more or less shrivelling. The same holds good of other reagents used cold, except Carnoy's solution, the fixing action of which, however, was not satisfactory. Killing with hot water, followed by treatment with various re-agents—Flemming without acetic, Henning, pierosulphuric, Hermann,—did not yield good results. On the whole the best sections so far have been obtained with specimens treated with hot sublimate-acetic. Double embedding (with either toluol-alcohol or alcohol-ether celloidin and paraffin) was found to be of advantage. Staining was most satisfactorily effected by means of haematoxylin (iron-alum method, Heidenhain, Delafield or Ehrlich) followed by erythrosin.

Most of the material available was collected by myself and fixed with hot sublimate-acetic. Though this was for the most part at least ten years old, it was in a good state of preservation. More recently, since I became engaged in this research, I have received highly valued assistance in the form of supplies of live crayfishes from Prof. H. G. Chapman and Mr. F. A. McNeill.

For comparison I have used species of *Tetranychus* and *Trombidium,* and various Hydrachnids, Tyroglyphids and Oribatids.

I am indebted to the University of Sydney for a grant from the McCaughey Research Fund which has defrayed the expenses incurred. My drawings have been re-drawn for the purpose of reproduction by Mr. F. W. Atkins of the Sydney Technical High School.

2. *Diagnosis of* Astacocroton.

Adult female imago permanently parasitic on gills of Crayfish, eyeless, incapable of swimming, devoid of tracheae. Integument of body thin, transparent, devoid of chitinous plates and practically hairless. Body swollen, ovoid, with the legs displaced forwards so as to be all in front of the middle of the trunk. Capitulum not greatly produced, with the mouth at the anterior end of its ventral surface. Chelicerae with the second joint piercing, barbed. Pedipalpi powerful, the last joint provided with hooked spines, the penultimate not produced. Epimera subequal, all distinct, except that the third and fourth are united for a very short distance at their inner ends; on the fused part but opposite the fourth, is the aperture of a gland or group of glands—coxal or integumentary. The legs are devoid of swimming hairs; each is armed terminally with a pair of strongly hooked tridentate claws. The genital aperture is a longitudinal slit close to the posterior extremity of the body. A little distance behind and above it is the excretory aperture. The animal is oviparous; a large number of ripe eggs, each enclosed in a thick shell, collect in the uterus, but their active development does not begin till after they have been discharged.

I propose to name the only species as yet known *A. molle.*

3. *General Features.*

The permanently attached females reach a maximum length of about 2 mm. When detached, full-grown specimens are able to climb about among the branchiae, but, when set free in water, they are unable to swim, though making energetic efforts to do so. Small specimens make more or less rapid progress through the water. The general shape is oval, with a slight ventral flattening. The integument is very thin, colourless and transparent, so that on the ventral side the ova and other internal structures are clearly visible. In some specimens the most conspicuous structures on this surface are a pair of rounded bodies, the "coxal glands" (Pl. xxxvi., fig. 1, *ex.*), situated between the bases of the fourth

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pair of legs. On the dorsal surface is a very conspicuous median longitudinal white band with irregularly lobed edges, marking the position of the excretory organ. This bifurcates in front and bifurcates also though less distinctly, behind. Towards the posterior end of the ventral surface is a narrow longitudinal slit bounded by a pair of chitinous plates set on edge—the reproductive aperture (Pl. xxxvi., fig. 1, *g.a.*; Pl. xxxvii., fig. 18). On either side of this extends a row of four "genital suckers" (Pl. xxxvii., fig. 18) each about .02 mm. in diameter, the row curved with the concavity inwards and set in a semi-lunar area which is apparently a thickening of the cuticle. A little distance behind the genital slit is the small, sometimes slit-like, sometimes rounded excretory aperture (Pl. xxxvi, fig. 1, *ex.a.*; Pl. xxxvii., fig. 18) with a slight raised rim. In addition to the mouth, to be described with the capitulum, the only other external apertures are those of the ducts of the coxal glands—a pair of minute pores .01 mm. in diameter on the coxae of the fourth pair of legs. There are no stigmata.

4. *Capitulum; appendages.*

In the larger specimens the capitulum (Pl. xxxvi., fig. 1, *ep*; fig. 2), is situated well behind the anterior margin, so as to be completely concealed from view when the animal is looked at from above. Its length is about one-fourteenth to about one-eighth of that of the body. Though it is freely movable, it is not definitely articulated with the body. Distally it is divided by a slight median notch, on either side of which are attached the bases of the pedipalpi. The mouth is situated on the ventral aspect of the distal end of the capitulum. It is a nearly circular aperture, bounded by a thick chitinous ring, continuous in front with the edges of a median slit between the bases of the pedipalpi. The area of the ventral surface of the capitulum behind the mouth is perforated by numerous extremely fine pores which, as sections show, perforate the cuticle.

The chelicerae, instead of lying in a groove on the upper surface as in the *Ixodidae* and *Bdellidae* and a few other *Acarida*, are roofed over by a continuation of the integument of the capitulum, as in *Trombidium* and the Hydrachnids, the entire basal joint being enclosed within the latter and the distal podomere alone being thrust out through the mouth.

Each chelicera (Pl. xxxvi., fig. 2, *ch₁*, *ch₂*; fig. 3) is composed, as in the majority of the Acarids, of two joints or podomeres, proximal and distal. The distal podomere is a sharp stylet, strongly curved, with the concavity dorsal and anterior. At a little distance from the point is an oblique flange strengthened by a sharp spine, the end projecting like a tooth; this must play the part of the barb of a hook in hindering withdrawal when a gill filament has been pierced. A second smaller oblique spine appears nearer the apex. Close to the point is a minutely serrated ridge of somewhat variable extent. Along the inner side runs a longitudinal flange extending from the base to near the apex. In the normal relations of the parts, with the two chelicerae in close apposition, their two longitudinal flanges combine to complete a longitudinal canal for the passage of the blood of the crayfish to the mouth of the parasite. The base of the distal joint lies within the mouth and is incapable of protrusion. It is expanded and divided into two condyles for articulation with the proximal joint and for the insertion of the muscles arising within the latter. Sections show that it is hollow, being pierced by a canal which opens into the cavity of the proximal joint by a fine aperture at the base between the two condyles. The canal contains a core of tissue, which, though the structure is not clear in any of my sections, is probably a duct opening near the distal end. The gland of which this would

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seem to be the duct is a granular mass contained in the cavity of the proximal joint between the muscles. It consists of a number of lobes which converge towards the distal end to form a vesicle which narrows to form the duct. The proximal joint may be described as oval, somewhat compressed laterally, and narrowing distally. Its long axis is not parallel with that of the capitulum, the proximal end being dorsal to the pharynx and the distal near the mouth. At its oral end it lies in the roof of the mouth cavity, and behind that it develops a knob which articulates with the chitinous element which I propose to term the *fulcrum*. The fulcra are of general, if not universal, occurrence in the Acaridae; but they do not appear to have had any name given to them that could be of general application. In tracheate forms such as *Trombidium* and the tracheate Hydrachnids they are hollow, the cavity which each encloses being in continuity with the tracheal system. In this connection they are termed the "drittes kieferpaar" by Haller (1881) "sigmoid chitinous piece" by Michael (1895) "zweite Luftkammer" by Henking (1882). Each not only supports the corresponding chelicera, but gives origin to the muscles by the contraction of which the movements of the latter, as a whole, are effected. The fulcra articulate with the chitinous "bridge." The middle part of the latter lies on the aboral side of the salivary receptacle in which the right and left main salivary ducts unite to open into the mouth. It is produced downwards and outwards in two strong chitinous bars which fuse with the cuticle at the lateral wall of the capitulum at its base. The fulcra in *Astacocroton* are strong, solid, curved rods of dense chitin, which, originating close together where they articulate with the chelicerae and the bridge, diverge as they pass backward and downwards like the limbs of an inverted V. From each arises a set of muscles passing backwards and upwards to be inserted into the proximal end of the basal podomere of the corresponding chelicera. When these muscles contract they must cause the rotation or tilting forwards in the vertical plane of the chelicerae on the fulcra, and this must result in the movement by which the harpoon-like free ends are made to pierce the gill of the crayfish.

In general it may be said that the structure of the capitulum and the chelicerae agrees well with that of these parts in *Trombidium* and the Hydrachnida. The most noteworthy difference seems to lie in the fulcra. In *Trombidium* and the tracheate Hydrachnids, instead of being solid rods, these, as already stated, are hollow and dilated into the form of air-chambers with chitinous walls connected with the tracheal system, while still retaining the same essential relationship with the bridge, the chelicerae and their muscles.

The pedipalpi (Pl. xxxvi., fig. 1, *pd*; figs. 4 and 5) are a little longer than the capitulum, stout, composed of five joints or podomeres, of which the second is the largest. The last, which is much narrower than the rest, is provided terminally with six spines, four of which are hooked; the penultimate bears a spine on the inner side of the distal end. The entire appendage is habitually curved downwards in adaptation to its function of grasping the gill-filaments and suspending the parasite.

The position of the legs (Pl. xxxvi., fig. 1) in the full-grown animal is a very marked feature, the last pair being far in front of the middle of the body—in fact, in large specimens not more than about a fifth of the entire length from the anterior end. This is associated with the great distension of the body with the ingested crayfish blood and the accumulated mass of eggs, but begins at a very early stage. The epimera (coxae) are subequal, the fourth a little longer than the rest, in contact with one another by their edges, but not fused, except the

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third and fourth, and these only for a short distance at their outer ends. In length the legs increase from before backwards, the fourth being much the longest and about half the length of the body in a large specimen. Each consists, as in other mites, of six podomeres (Pl. xxxvi., fig. 6) in addition to the epimeron. Swimming hairs are not developed on them, there being only a small number of short hairs. At its extremity (Pl. xxxvi., fig. 7) each is provided with a pair of strongly-hooked trifid or tridentate claws without sucking disk, but with a stoutish spine.

5. *Coxal or integumentary glands.*

The two oval bodies referred to above as the coxal glands may not correspond to the organs so named in other Arachnids, and the name is mainly applied to them here on account of the position of the openings of their ducts on the coxae of the last pair of legs. The "glands" in question (Pl. xxxvi., fig. 1, *cx*) are situated close to the ventral surface behind the central nervous system. Each is divided into about half-a-dozen lobes which converge outwards and forwards towards the point from which the duct is given off, and narrow prolongations of some extend into the latter and may reach the aperture. The clear substance of which these lobes are composed is very hard in the preserved specimens and in many cases refused to be cut into sections, the gland breaking into irregular pieces and tearing up adjoining structures. In one series of sections, however, of an immature female without eggs, it is clear enough that each lobe is divided transversely by thin partitions into several (usually four) parts, and that in each of these is a small round body like an indistinct nucleus. On the other hand in some series of sections of full-grown specimens with numerous eggs the organ has not broken and the sections of it appear like sections of an almost homogeneous body, staining strongly and uniformly with eosin or erythrosin, and without histological structure. In the smallest specimens which I have obtained—minute free-swimming stage—the organs in question are very distinctly divided into lobes and have wide ducts, but the specimens, mounted whole unstained, are not in a condition to show minute structure. The conclusion to be derived from the imperfect data appears to be that, while probably functional in the young animal, these glands become inert in the fixed parasite and their histological structure degenerates.

Openings of "integumentary glands" are present on the fourth epimera in *Teutonia, Limnesia* and *Limnesiopsis* (Piersig u. Lohmann, 1901). It seems probable that the glands in question are of the same nature as the bodies above described; but the latter appear to be very different from the dorsal integumentary glands described by Michael (1895) and others in *Thyas* and various other Hydrachnids.

6. *Digestive System.*

A slit between the bases of the pedipalpi expands behind into the rounded aperture of the mouth which is surrounded by a ring-like thickening of the cuticle. The latter is produced inwards to form the investment of the buccal cavity. The latter gives off the pharynx almost immediately within the mouth-opening (Pl. xxxvi., fig. 8), and is continued below the basal joints of the two chelicerae into a dorso-ventrally compressed space which expands laterally and receives at its outer angles the main salivary ducts. This space, which may be termed the *salivary receptacle* (*s.r.*), is separated from the buccal cavity proper by a fold of the thin membrane forming the floor of both, a fold which lies on a cushion-like elevation and may act as a valve.

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6. *Digestive System.*

A slit between the bases of the pedipalpi expands behind into the rounded aperture of the mouth which is surrounded by a ring-like thickening of the cuticle. The latter is produced inwards to form the investment of the buccal cavity. The latter gives off the pharynx almost immediately within the mouth-opening (Pl. xxxvi., fig. 8), and is continued below the basal joints of the two chelicerae into a dorso-ventrally compressed space which expands laterally and receives at its outer angles the main salivary ducts. This space, which may be termed the *salivary receptacle* (*s.r.*), is separated from the buccal cavity proper by a fold of the thin membrane forming the floor of both, a fold which lies on a cushion-like elevation and may act as a valve.

The pharynx (Pl. xxxvi., figs. 8-10, *ph*; Pl. xxxvii., figs. 11-12) has the general structure usual in the *Acarida*, corresponding closely in most respects with that of *Trombidium* as described by Henking and that of *Thyas* as described by Michael. An important difference, however, is that the swallowing muscles ("Schluckmuskeln" of Henking, "transverse muscles" of Michael) which are so conspicuous in transverse sections of this region in *Trombidium* and occur also in the Hydrachnids, or at least in some of them, are here entirely absent—the sucking muscles being opposed merely by the elasticity of the wall of the pharynx. The chief agents in the sucking action are the "dilatores pharyngis" muscles of Michael (1895, p. 182). To the result of the contraction of these muscles in enlarging the lumen of the pharynx, a contribution is made by short muscular bundles arising from the inner surface of the ventral cuticle in the middle line and inserted into the ventral half-tube of the pharynx, mainly into a keel-like process which projects downwards from the latter; this muscle which may be termed *depressor pharyngis*, is figured by Michael in *Thyas* (1895, fig. 23), but is not lettered and is not mentioned in the text.

The "Giftdrüsen" which are also very conspicuous in transverse sections of the capitulum of *Trombidium* and are described and figured in that genus by Henking (1882) are entirely absent in *Astacocroton*. So also is the azygous gland referred to by Michael (1895, p. 192) as lying (in *Thyas*) between the two sets of muscles which tilt up the chelicerae.

There is, however, in this region, a gland (?) not represented in *Trombidium* and not recorded, so far as I can ascertain, as occurring in any other Acarid. This, which I propose to name pharyngeal gland, is rather (if it be indeed glandular) of the nature of a group of large unicellular than of a pair of compound glands. These (Pl. xxxvii., fig. 12, *g*) are situated between and around the dilator muscles of the pharynx. Each is a somewhat pyramidal cell, 0.1 mm. in length, with a rounded base directed upwards, and the attenuated apex becoming lost among the fibres of the dilator muscles near the dorsal wall of the pharynx. Each cell has a nucleus about .01 mm. in diameter, and vacuolated cytoplasm which is not readily affected by stains.

The oesophagus is extremely narrow, with an excessively minute lumen. As usual it perforates the central nerve-mass to open into the mesenteron. The latter consists of an anterior median sac extending across the whole breadth of the body immediately behind the dorsal salivary gland, and a pair of caeca which extend back to the posterior end of the body. As in the *Prostigmata* in general, there is no hind-gut or anus. The two caeca (Pl. xxxvii., figs. 14-16, *ent*) are separated from one another by the median excretory organ (*ex*) and occupy with it all the dorsal part of the cavity of the body—the ventral part being taken up by the ovary and the uterus. The median sac and the caeca are of essentially the same structure. A basement membrane supports an epithelium of an extremely irregular character. The contents are invariably the blood of the crayfish, disseminated through which are usually to be seen numbers of the characteristic blood-corpuscles.

The epithelium resembles the corresponding layer in the Acarida in general as described by Michael (1895, 1894-97), Thor (1904) and others. Some of the cells are relatively small, others are produced into the lumen and dilated distally, the proximal part usually becoming constricted. The protoplasm of the large cells and, to some extent, of the small also, is loaded with a variety of metaplasmic bodies, in the form of granules, spherules and irregular concretions, which vary very greatly in character and relative abundance in different individuals.

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As appears to be very generally the case in the Acarida (Michael, 1895, 1894-97; Thor, 1904), as well as in some other Arachnids (Bernard, 1894), the cells or portions of them, often become free in the lumen. As the contained blood remains uncoagulated they are able to float freely, but in a few of my series, the blood has for some reason undergone coagulation while the animal was still alive, and in these cases the passage of the wandering cells from one side to the other is plainly indicated by clean-cut cylindrical burrows through the coagulum (Pl. xxxvii., fig. 14). The definitiveness of these and their straight, or nearly straight, course, seem to indicate a distinct attraction or repulsion—not due to gravity, since the direction of the canals is not the same on opposite sides. In a specimen crushed while alive, moving enteric cells can sometimes be distinguished. These assume the elongated narrow shape which they most habitually adopt in traversing the enteric lumen.

The crayfish blood-corpuscles are ingested by the cells of the enteric epithelium. This is quite clear in only one of my series of sections—one in which the corpuscles are very strongly stained and the blood plasma and endoderm cells not too strongly. It is certain of the latter projecting far into the lumen or altogether detached that mainly discharge this function. In successive sections of one of these cells I have counted as many as fifty of the corpuscles, some adhering to the surface, others half embedded, others more or less deeply sunk in the cell-protoplasm.

There are no intrinsic muscles in the wall either of the mesenteron or of the excretory organ, and yet in the living animal, contractions occur in waves at irregular intervals in the walls of both mesenteron and excretory organ. These contractions must be due to a pair of strong muscular bands which extend obliquely throughout the length of the body from the dorsal body-wall above the anterior extremity of the excretory organ backwards and downwards, one on either side of the excretory organ, between it and the corresponding mesenteric caecum, to the neighbourhood of the excretory aperture.

7. *Salivary and anti-coagulin Glands.*

There are in *Astacocroton* three pairs of glands representing the "salivary" series. If we adopt Thor's (1904, p. 105) nomenclature, these would correspond to his *tubular*, *reniform* and *dorsal*—the last being perhaps the equivalents of both anterior and posterior dorsal pairs, or perhaps of only one of them. The anterior and posterior oesophageal pairs and the unpaired tracheal are not represented.

By far the largest of these are the last—the *dorsal*. These are about .3 mm. in diameter, situated dorsally at the extreme anterior end of the body, just behind the bases of the chelicerae, dorsal to the oesophagus and nerve-centre, fitting close down over these structures and in close contact with one another in the middle line. Each consists (Pl. xxxvii., fig. 13) of a group of large cells, about .2 mm. in length, of approximately pyramidal shape, arranged around a central cavity of variable extent—the beginning of the duct (*d*)—which is bounded by their apices and is lined by a thin cuticle. Towards the broader end each cell is composed of an almost homogeneous substance which is not very strongly affected by staining agents; but, invading this near the apex, and sometimes spreading throughout the greater part of the cell, is the accumulating secretion, which in lightly stained sections appears clear and yellowish, but in such as have been strongly eosinated shows as masses of rounded granules. Each cell has a large nucleus, .03 mm. in diameter, with a spheroidal nucleolus, .01 mm. in diameter,

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and an achromatic network having a prevailingly radial arrangement. The narrow apical part of each cell is virtually its duct and pierces the cuticle of the beginning of the main duct to open into its lumen. In large adult animals the structure becomes complicated by the main duct receiving a tributary duct, which arises from a small cavity of the nature of a secondary lumen in the interior of the more ventral part of the gland.

The duct, a narrow tube with a cuticular lining, runs straight forwards to join those of the two glands yet to be described.

The *reniform* glands (Pl. xxxvi., fig. 10 and Pl. xxxvii., fig. 13, S_2) are much smaller than the dorsal—only about .07 mm. in diameter—and lie opposite the middle of the dorsal glands and external to the latter. The main part of each is a rounded body containing a number of nuclei which, though large (.01 mm. in diameter) compared with those of most of the other tissue-elements, are small in comparison with those of the dorsal glands. These nuclei are quite irregularly arranged and the cells which they represent are not always clearly distinguishable. In the substance of the gland are small vacuoles and canals and a narrow central lumen, not distinguishable in all cases, from which the duct arises. The latter runs forwards to join the other salivary ducts.

The third pair of glands in *Astacocroton* belonging to the "salivary" group—the *anti-coagulin* glands—undoubtedly correspond morphologically to the "tubular salivary glands" of Michael, the "glandes tubulaires" of Thor, the "schlauch-förmige Drüsen" of Schaub (1888). But in *Astacocroton* these glands present features of significance which, so far as I can ascertain, have not been observed in any other Acarid. Each gland (Pl. xxxvi., fig. 10, *co*) begins in front close to the corresponding dorsal and reniform glands, external to the former and separated from it by the muscles running from the dorsal body-wall to the base of the rostrum, somewhat ventral to and behind the latter. The anti-coagulin gland begins in front in an elongated vesicle or reservoir with, in some cases, a considerable lumen and comparatively thin walls. This gives off, in front, a duct which runs inwards and forwards to join those of the reniform glands. Posteriorly it is produced into a tube which is thrown into several folds, and undergoes several dilatations. The chief of these dilatations has a funnel-like appearance in transverse sections. What represents the mouth of the funnel, which faces inwards, is closed by a thin wall of small cells. The remaining walls of the "funnel" are relatively thick and composed, like the rest of the organ, of cells without definite boundaries, recognisable only by their nuclei which are distinctly smaller than those of the reniform glands. The reservoir passes into a wide tube which is twisted on itself and this divides behind into two narrow tubes (about .03 mm. in diameter) which run backwards in the wall of the mesenteron (Pl. xxxvii., fig. 15, *a.c.g.*) sometimes close together, sometimes wider apart. Finally, far back in the wall of the mesenteric diverticulum, the two tubes unite and terminate; in other words, the two tubes are in reality a loop. In some series there is a short anastomosis about the middle.

The meaning of the special form of the tubular glands and the peculiar position of their loops might be conjectured; but to my mind at least it is rendered perfectly clear by the evidence of some of my series of sections. In these, not only is the mesenteric epithelium altered and partly dissolved away along the track of the loop, but a definite effect has evidently been in the act of being produced on the blood in the mesenteric lumen, an effect which is strictly limited to this track and extends throughout its length. The nature of this effect is difficult to describe: it is as if a cloud of clear unstainable liquid were

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passing out into the faintly stainable granular plasma of the blood-food along the course of the loop. The conclusion seems unavoidable that, though the tubular glands have their own ducts which carry their secretion into the month through the common salivary duct, a part of the secretion diffuses from the looped tube into the lumen of the mesenteron.

That an anti-coagulin is produced in the digestive system of *Astacocroton* has not been proved. In the ticks *Ixodes* and *Argas*, Sabbatani, in the case of the former, and Nuttall and Strickland (1908) in the case of the latter, demonstrated its presence experimentally. But since the question presented itself I have not been able to muster sufficient fresh material to render such experiment practicable. However, the fact that the blood-food does remain uncoagulated in all but a few exceptional cases seems to prove that an anti-coagulin is produced. And the very peculiar relationship found to exist between the loop of the tubular gland and the mesenteric epithelium seems to point to that gland as the most probable source of the ferment.

8. *The integument; the so-called fat-body.*

The cuticle of the general surface is very thin—about .00143 mm.—It consists of two layers—the outer homogeneous, the inner with an obscure structure of vertical pillars, with an undulated inner surface. That of the capitulum is nearly twice as thick. The underlying layer—epidermis—is thinner than the cuticle, and in the adult animal no longer exhibits a cellular structure. Below the epidermis, in the body-cavity are a good many leucocytes, about .01 mm. in diameter when rounded off, filled with small granules, which have a strong affinity for eosin or erythrosin.

Within, on the dorsal side, is a layer (Pl. xxxvii., figs. 15 and 16, *f*) not quite continuous, of sharply defined cells of irregular shape and size, averaging about 0.02 mm. in diameter with nuclei of about 0.01 mm. and nucleoli of about 0.005 mm. or rather less.

These are the cells figured and described in *Trombidium* by Henking (1882, Plate xxxiv., fig. 10) as "Fettkörperzellen." They lie in close contact with the dorsal side of the mesenteron and excretory organ, and in front of these over the dorsal glands. Thor (1904, p. 37) regarded them erroneously as young ova.

9. *The Excretory Organ.*

This is a median sac (Pl. xxxvii., figs. 14-16, *ex*) extending throughout the length of the body towards the dorsal side, and opening on the exterior by the small excretory aperture (Pl. xxxvi., fig. 1 and Pl. xxxvii., fig. 18), situated a little distance behind the posterior end of the genital slit. In front it divides into two branches which curve outwards and forwards each running in an almost transverse direction in a fold of the wall of the mesenteron to terminate blindly over the coxal glands. Behind, before narrowing to open on the exterior, it gives off a pair of short lobed caeca. Its general appearance in the living animal has already been referred to. In sections the main part of the organ is seen to be a laterally compressed tube with a narrow vertical lumen expanding somewhat dorsally where it lies immediately below the dorsal body-wall. It is intercepted between the two enteric caeca, with the inner walls of which it is intimately connected, and abuts below on the wall of the uterus.

The wall of the organ consists of two layers only—an internal epithelium and an external supporting layer or basement-membrane. The epithelium is a single layer of cells flattened for the most part and not sharply marked off from

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10. *Reproductive system.*

The female genital aperture has, as already stated, a form which is very usual in the Acarids, viz., that of a longitudinal slit bounded by a pair of vertically-placed chitinous plates. The passage (vagina) into which it leads is surrounded by a thick mass of muscular fibres, and the cavity is almost obliterated in most sectioned specimens by the close apposition of the lateral walls. In front the cavity opens out and then bifurcates, each of the two lateral vaginae thus formed opening into the corresponding division of the uterus.

In young specimens in which there are no fully formed ova and in which the uterus is empty, the latter is divided, except in front, into right and left cavities by a median vertical partition. In mature specimens with the uterus packed with eggs, this partition only remains complete in the posterior region; further forward it breaks down, only a remnant at most at its dorsal part persisting. Further forward still it completely disappears and the uterus presents an undivided cavity.

The wall of the uterus is composed of a single layer of cells supported upon a basement membrane. In the mid-ventral region the latter alone persists. In the lateral regions the cells become vertically elongated. It must be to the activity of these cells that the formation of the thick and complicated egg-shells is due, since there are no other elements that could be concerned in this process.

The ovary (Pl. xxxvii., figs. 15 and 16, *ov;* fig. 17) lies mainly on the ventral side of the uterus with the ventral wall of which, here for the most part composed merely of basement membrane, it is intimately united. But in front it extends round it to the dorsal side and is prolonged a little distance in front of it in the region just behind and between the coxal glands. The ova, developed in the substance of the ovary in the manner subsequently described, then projecting outwards in the stalked stage, later become free in the surrounding cavity (which is simply the body-cavity) and there grow to their full size. Communication between the body-cavity and the interior of the uterus is effected by a pair of apertures situated far forward just behind the coxal glands. The free (outer) surface of the ovary is covered with a very thin layer (not definitely represented in Pl. xxxvii., fig. 17) which is prolonged over each of the developing ova—Henking's *tunica propria ovarii.*

Although it is impossible to follow the details of the oogenesis in the material at present available, there are a few important points to be noted. The ova appear in the substance of the ovary—a layer about .05 to .07 mm. in thickness. The cells, as they near the outer surface, become separated into two sets—(1) those destined to become ova and (2) those destined to become stalk-cells. The former become larger and come to project on the free surface. The latter remain small with denser protoplasm and very small nuclei, and form groups of about five or six beneath the growing ova. Each group is developed into a stalk with about a dozen nuclei, embedded at its base in the substance of the ovary, but quite sharply cut off from the latter, and bearing a young ovum at its free end. Such a stalk probably plays the part of a nutrient organ, re-

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In young specimens in which there are no fully formed ova and in which the uterus is empty, the latter is divided, except in front, into right and left cavities by a median vertical partition. In mature specimens with the uterus packed with eggs, this partition only remains complete in the posterior region; further forward it breaks down, only a remnant at most of its dorsal part persisting. Further forward still it completely disappears and the uterus presents an undivided cavity.

The wall of the uterus is composed of a single layer of cells supported upon a basement membrane. In the mid-ventral region the latter alone persists. In the lateral regions the cells become vertically elongated. It must be to the activity of these cells that the formation of the thick and complicated egg-shells is due, since there are no other elements that could be concerned in this process.

The ovary (Pl. xxxvii., figs. 15 and 16, *ov;* fig. 17) lies mainly on the ventral side of the uterus with the ventral wall of which, here for the most part composed merely of basement membrane, it is intimately united. But in front it extends round it to the dorsal side and is prolonged a little distance in front of it in the region just behind and between the coxal glands. The ova, developed in the substance of the ovary in the manner subsequently described, then projecting outwards in the stalked stage, later become free in the surrounding cavity (which is simply the body-cavity) and there grow to their full size. Communication between the body-cavity and the interior of the uterus is effected by a pair of apertures situated far forward just behind the coxal glands. The free (outer) surface of the ovary is covered with a very thin layer (not definitely represented in Pl. xxxvii., fig. 17) which is prolonged over each of the developing ova—Henking's *tunica propria ovarii.*

Although it is impossible to follow the details of the oogenesis in the material at present available, there are a few important points to be noted. The ova appear in the substance of the ovary—a layer about .05 to .07 mm. in thickness. The cells, as they near the outer surface, become separated into two sets—(1) those destined to become ova and (2) those destined to become stalk-cells. The former become larger and come to project on the free surface. The latter remain small with denser protoplasm and very small nuclei, and form groups of about five or six beneath the growing ova. Each group is developed into a stalk with about a dozen nuclei, embedded at its base in the substance of the ovary, but quite sharply cut off from the latter, and bearing a young ovum at its free end. Such a stalk probably plays the part of a nutrient organ, re-

placing the cells of the nutrient chambers of the ovaries of certain Insects. But before the ova have increased greatly in size, and long before the yolk has begun to be formed, the ovum has developed over its entire surface a definite though thin membrane with the appearance of chitin, which cuts off the stalk and must interfere to some extent with free absorption. The original investment meanwhile disappears. The younger stalked ova (Pl. xxxvii., fig. 17, 1-4) are quite devoid of yolk, but each contains in its cytoplasm a mass of substance having staining reactions very similar to those of chromatin. This, corresponding to a "yolk-nucleus," at first surrounds, or partly surrounds, the nucleus; then becomes aggregated on one side assuming a variety of forms usually analysable into twisted anastomosing threads. Later it becomes broken up into small masses and dispersed through the cytoplasm, and long before the detachment of the ovum from its stalk, yolk-spherules make their appearance. At first they are only developed in the outer zones, leaving a large, sharply defined, yolkless central area (Pl. xxxvii., fig. 17, 5); but later they extend uniformly throughout the protoplasm and increase greatly in size from .002 mm., when first clearly distinguishable, to .015 mm. in the ripe egg.

How and at what stage fertilization takes place has not been ascertained, nor has any trace been seen of maturation phases. When the ovum enters the uterus it at once becomes enclosed in a thick shell secreted by the elongated epithelial cells of the lateral parts of the uterus. The completed egg is .23 mm. in diameter. The egg shell is about .015 mm. in thickness and consists of three layers, an outer very thin, a middle, the thickest, made up of radially elongated rod-like elements, and an inner which is the original chitinous investment of the ovum. About fifty of these ripe eggs accumulate in the uterus of a mature female. Their further history has not yet been followed.

The relations between the ova, the body-cavity and the uterus in *Astacocroton* seem, if we have regard to the statements in general works such as Warburton's "Arachnids" of the "Cambridge Natural History," or Marie Daiher's "Arachnoidea" of Lang's "Lehrbuch," to be quite without parallel in the Arachnida; but if we look more closely into the descriptions and figures of certain of the original papers we are forced to the conclusion that the relations in question must in certain other groups of the *Acarida* be essentially the same as in *Astacocroton*.

Thus in his account of *Bdella* Michael (1894-97, p. 516) states "The ova are formed and more or less matured in short pedunculated cysts, each ovum apparently forming its own oocyst by pushing out the exterior tunic of the ovary, thus forming a sac in which the ovum lies. Exactly how the ovum gets from the oocyst into the oviduct is not by any means clear to me in *Bdella*, or, indeed in many of the other Acarina, although it is evident in the Oribatidae and most Gamasidae."

His figures 24 and 25 show clearly enough that before the ova represented can reach the interior of the oviduct they must first become detached from their peduncles and enter by apertures in the wall of the oviduct or uterus. Precisely the same holds good of Henking's (1882) Figs. 14-16, representing the female reproductive apparatus of *Trombidium*.

Under the heading "Glands of unknown function" Michael (1895) in his account of *Thyas petrophilus* describes as follows a pair of glands which occur in both sexes:—

"Lying immediately below the lateral portions of the hollow square of the ventriculus immediately above the genital organs in both sexes, and about the middle longitudinally of the latter organs, exist a pair of almost globular or

placing the cells of the nutrient chambers of the ovaries of certain Insects. But before the ova have increased greatly in size, and long before the yolk has begun to be formed, the ovum has developed over its entire surface a definite though thin membrane with the appearance of chitin, which cuts off the stalk and must interfere to some extent with free absorption. The original investment meanwhile disappears. The younger stalked ova (Pl. xxxvii., fig. 17, 1-4) are quite devoid of yolk, but each contains in its cytoplasm a mass of substance having staining reactions very similar to those of chromatin. This, corresponding to a "yolk-nucleus," at first surrounds, or partly surrounds, the nucleus; then becomes aggregated on one side assuming a variety of forms usually analysable into twisted anastomosing threads. Later it becomes broken up into small masses and dispersed through the cytoplasm, and long before the detachment of the ovum from its stalk, yolk-spherules make their appearance. At first they are only developed in the outer zones, leaving a large, sharply defined, yolkless central area (Pl. xxxvii., fig. 17, 5); but later they extend uniformly throughout the protoplasm and increase greatly in size from .002 mm., when first clearly distinguishable, to .015 mm. in the ripe egg.

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"Lying immediately below the lateral portions of the hollow square of the ventriculus immediately above the genital organs in both sexes, and about the middle longitudinally of the latter organs, exist a pair of almost globular or

slightly elliptical, organs of about .04 mm. diameter in the male and about .05 to .1 mm. in the female. These organs (fig. 19, *gu*) have every appearance of being glands; they are composed of distinctly nucleated closely-packed elongated cells of about .01 mm. diameter and in section exhibit similar cellulation all through; they are quite solid without lumen, but I have not been able to trace any duct from them. I thought at one time that they probably discharged into the posterior part of the tubular salivary glands, but after careful investigation I am not, up to the present, able to state that this is the case, although the two organs are in tolerably close juxtaposition; and the function of the glands therefore remains uncertain to me" (1895, p. 197).

A pair of organs which are almost certainly homologous with those described occur in the female *Astacocroton*. They are a pair of rounded organs nearly .2 mm. in diameter, ventro-laterally situated between the mesenteric diverticulum and the uterus, embedded in the posterior wall of the latter. Each is a solid mass of polyhedral cells averaging about .02 mm. in diameter, without lumen and without duct. There is certainly no connection with the tubular salivary gland, the bend of the loop of which is definitely anterior. There is a very close association between the cells of this gland and those of the uterine epithelium, but if the former organ occurs, as Michael states it does in *Thyas*, in both sexes, its function is not easy to determine. In the only male *Astacocroton* (immature) of which I have sections it was not seen.

11. *Male.*

I am not in a position to give a full account of the male since I have only a single specimen, and that is in an immature condition. I have never found a male attached to the gills—the few I have seen being free in the gill-cavity. Their apparent scarcity may be partly due to their freedom. The specimen referred to was very small, not more than a millimetre in length. The appendages are not distinguishable from those of the female. The presence of a pair of eyes may be peculiar to the male; but early stages of the female may possess them. The chief—if not the only—external difference distinguishing the male is in the reproductive aperture, which is a comparatively short slit situated relatively far forward, about the middle of the ventral surface.

Sections of this specimen show that the reproductive apparatus is still in a very rudimentary condition. The testes are a pair of sacs with distinct empty lumina. These open in front into a narrow median passage (vas deferens) leading to the genital aperture. Behind they unite together in the middle line, their cavities communicating. The two testes and their connections thus form a kind of ring. The walls of the testes are composed of a mass of minute cells of uniform character. Accessory glands are recognisable as a group of cells about the median vas deferens and its external aperture. In the mature condition it is obvious that the lumina of the testes will act as vesiculae seminales, and their continuation to the median vas deferens as the lateral vasa deferentia.

12. *Conclusion.*

It appears to be almost certain that the nearest relatives of *Astacocroton* are to be looked for among the Hydrachnida; no mite not adapted to aquatic life could conceivably have given origin to a permanent external parasite of an aquatic animal. The marine derivation of such a hypothetical non-parasitic or partly parasitic ancestor is not necessarily excluded. Living alongside *Astacocroton* in the gill-cavity of the crayfish is *Stratiodrilus*, whose only known relative

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—and that quite a near one—lives on European lobsters (*Nephrops* and *Homarus*). But structurally the marine Hydrachnid genera—*Pontarachna* and *Nautarachna*—seem less remote than the rest of the marine Acarids—the Halacaridae.

Such cases of parasitism as are known in the Hydrachnids have little analogy with the case of *Astacocroton*. Many of them are cases in which the parasitism is confined to the larval stage. In the case of various species of *Atax* and of *Naiadicola ingens*, in which the young become parasitic on the gills of fresh-water mussels, the parasitism may be continued to the adult condition. But there is nothing to connect any of these structurally with *Astacocroton*; if that genus is to be set down as a parasitic Hydrachnid, it seems to have no close relationship with any Hydrachnid hitherto known.

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Lettering.

a.c.g. (in fig. 15) supposed anti-coagulin glands; *b.c.* buccal cavity; *br.* bridge;
ch_1, ch_2, basal and terminal joints of chelicerae; *ch.m.* muscles running from fulcra
to chelicerae; *ent.* enteron; *ex.* excretory organ; *ex. a.* excretory aperture; *ex.* coxal
gland; *f.* "fat-body"; *fu.* fulcrum; *g.* pharyngeal gland; *l.n.* lateral nerve (in
capitulum); *m.n.* median nerve (in capitulum); *mus.* dorso-ventral muscle even-
tually inserted into base of capitulum; *ov.* ovary; *pd.* pedipalpi; *pd.m.* muscles to
base of pedipalpi; *ph.* pharynx; *pi.* undetermined pigmented body; *r.m.* retractor
muscle of chelicera; s_2 reniform salivary gland; *s.r.* salivary receptacle; *u.* uterus.

EXPLANATION OF PLATES XXXVI.-XXXVII.

Plate xxxvi.

Fig. 1. Female; general ventral view ($\times$ 30).

Fig. 2. Ventral view of capitulum and chelicerae ($\times$ 225) with outlines of
basal parts of chelicerae, bridge and pharynx seen through the integument; pedi-
palpi not shown.

Fig. 3. Second podomeres of chelicerae as seen *in situ* slightly separated by
pressure and turned in slightly different directions ($\times$ 520).

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anti-coagulin gland; *d.* duct of dorsal salivary gland; *d.m.* depressor muscle of
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base of pedipalpi; *ph.* pharynx; *pi.* undetermined pigmented body; *r.m.* retractor
muscle of chelicera; s_2 reniform salivary gland; *s.r.* salivary receptacle; *u.* uterus.

EXPLANATION OF PLATES XXXVI.-XXXVII.

Plate xxxvi.

Fig. 1. Female; general ventral view ($\times 30$).

Fig. 2. Ventral view of capitulum and chelicerae ($\times 225$) with outlines of
basal parts of chelicerae, bridge and pharynx seen through the integument; pedi-
palpi not shown.

Fig. 3. Second podomeres of chelicerae as seen *in situ* slightly separated by
pressure and turned in slightly different directions ($\times 520$).

Figs. 4 and 5. Views of extremity of pedipalpi (× 525).

Fig. 6. Fourth leg.

Fig. 7. Extremity of leg (× 525).

Fig. 8. Approximately sagittal section of capitulum (× 225).

Fig. 9. Transverse section of the capitulum passing through the bridge and the salivary receptacle (× 225).

Fig. 10. Semi-diagrammatic outline of the nerve-mass, the anti-coagulin gland of the left side, and adjoining parts. The dorsal salivary gland and the main duct are indicated by the broken lines, the main salivary duct by the dotted lines.

Plate xxxvii.

Fig. 11. Transverse sections of capitulum behind the middle part of the bridge (× 225).

Fig. 12. Similar section a little further back.

Fig. 13. Section of dorsal salivary gland from a transverse series.

Fig. 14. Transverse section of the right enteric caecum and the adjacent median excretory organ. The shaded body in the interior of the former represents the mass of crayfish blood with the channels excavated in it. The details of the boundaries of the cells in this and the two following figures are not given.

Fig. 15. Transverse section of young animal without any full-grown ova and the uterus empty. The blood filling the enteric caeca is not represented: the integument is indicated by a single line. The uterine partition has disappeared in the region represented.

Fig. 16. Similar sections of a mature specimen with the uterus distended with ripe eggs, one only of which is represented (× 40).

Fig. 17. Portion of a section through the ovary, showing various stages in the development of the stalked ova, the "yolk-nucleus," and its replacement in the largest ovum by the yolk spherules (× 525).

Fig. 18. Genital aperture, genital suckers and excretory aperture (× 120).

Figs. 4 and 5. Views of extremity of pedipalpi (× 525).

Fig. 6. Fourth leg.

Fig. 7. Extremity of leg (× 525).

Fig. 8. Approximately sagittal section of capitulum (× 225).

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